Available online at www.sciencedirect.com
ScienceDirect
Vision Research 46 (2006) 3831–3844
Vision Research
www.elsevier.com/locate/visres

Effect of previously fixated locations on saccade trajectory during free visual search

Hiroyuki Sogo *, Yuji Takeda

Institute for Human Science and Biomedical Engineering, National Institute of Advanced Industrial Science and Technology, AIST Tsukuba Central 6, 1-1-1 Higashi, Tsukuba, Ibaraki 305-8566, Japan

Received 1 March 2006; received in revised form 7 July 2006

Abstract

Recent studies have shown that the saccade trajectory often curved away from an object that was previously attended but irrelevant to the current saccade goal. We investigated whether such curved saccades occur during serial visual search, which requires sequential saccades possibly controlled by inhibition to multiple locations. The results show that the saccade trajectories were affected by at least three previous fixations. Furthermore, the effect of the previous fixations on saccade trajectories decreased exponentially with time or the number of intervening saccades. The relationship between the curved saccade trajectory and inhibition of return during serial visual search was discussed.

Keywords: Visual search; Saccade trajectory; Inhibition of return

1. Introduction

Saccades play an important role in the exploration of complex visual scenes in daily life. The ''premotor theory'' hypothesized that the programming of saccades and covert shifts of spatial attention are closely related to each other because of shared neural circuits that control them (Rizzolatti, Riggio, Dascola, & Umilta, 1987). Recent evidence supporting the premotor theory shows that spatial attention can modify the trajectory of a single saccade (Doyle & Walker, 2001; Godijn & Theeuwes, 2002, 2004; Sheliga, Riggio, & Rizzolatti, 1994, 1995; Sheliga, Craighero, Riggio, & Rizzolatti, 1997). In a typical paradigm (Sheliga et al., 1997), the participants were required to make a vertical saccade to a target located above or below a fixation point. Saccade direction was specified by a cue presented in one of four peripheral boxes located at the corners of an imaginary square around the fixation point. The participants directed their attention to the peripheral cue without any eye movements and then made a saccade to the specified target. In this condition, the saccade trajectory curved away from the cued box. The other studies also reported such curved saccade trajectories in various conditions. For example, curved saccade trajectories could be observed regardless of whether the saccade goal was determined endogenously (e.g., the saccade goal is pointed to by an arrow on a fixation point) or exogenously (e.g., the goal is indicated by a flash on the goal) in several studies (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga et al., 1997). Furthermore, auditory and tactile cues, as well as visual cues, also caused curved saccades (Doyle & Walker, 2002).

In the previous studies, the cause of curved saccade trajectories was explained as due to mutual inhibitory interactions between saccade commands (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga, Riggio, & Rizzolatti, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001). For example, Godijn and Theeuwes (2002) proposed a competitive integration model of saccade programming to explain curved saccade trajectories. Their model proposes that

* Corresponding author.
E-mail address: h-sogo@aist.go.jp (H. Sogo).

0042-6989/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2006.07.003

potential saccade goals are represented as localized activations on a single topological map (a saccade map). On this map, neighboring activations are combined to become a relatively stronger activation, while distant activations mutually inhibit each other. When one of the activation peaks reaches a threshold, a saccade whose dynamics are specified by the peak location is executed. In addition to mutual inhibition within the saccade map, their model proposes that the saccade map receives inhibitory endogenous input in order to prevent saccades to the undesired locations. In the paradigm of the curved saccade studies (e.g., Sheliga et al., 1995), the location of the cue should be inhibited on the saccade map because it is irrelevant to the location of the saccade goal. Because the inhibitory input pushes the peak of activation away from the inhibited location, the initial direction of a saccade would shift away from the inhibited location. This shift of the initial direction would be dynamically compensated by an internal feedback loop (Robinson, 1975; Sparks & Mays, 1983), resulting in a curved saccade trajectory away from the inhibited location (Lefèvre, Quaia, & Optican, 1998; McSorley, Haggard, & Walker, 2004).

These assumptions about curved saccade trajectories are consistent with previous studies on the superior colliculus (SC) in the midbrain. The SC includes a two-dimensional motor map that represents saccade vectors in a topological manner (Guitton, 1991; Leigh & Zee, 1999) and receives both excitatory and inhibitory inputs from cortical areas such as the frontal eye field (Segraves & Goldberg, 1987; Schlag-Rey, Schlag, & Dassonville, 1992), the dorsolateral prefrontal cortex and the posterior parietal areas (Selemon & Goldman-Rakic, 1988). Short-distance excitatory and long-distance inhibitory interactions have been found within the SC (Meredith & Ramoa, 1998; Munoz & Istvan, 1998). Applying subthreshold stimulation to the SC during a pre-saccadic period produces a saccade curved in the direction represented by the stimulated site (McPeek, Han, & Keller, 2003). On the other hand, microinjection of Muscimol (which inhibits neuronal activities near the injection site) into the SC produces a saccade curved away from the direction represented by the injection site (Aizawa & Wurtz, 1998; Quaia, Aizawa, Optican, & Wurtz, 1998). Although it is possible that several higher cortical areas are also involved in attentional modification of saccade trajectories, the SC is a plausible candidate for the neural correlate of such attentional modification.

The primary interests of the present study are determining whether systematic curved saccade trajectories are found using cognitive tasks similar to those performed in daily life, and whether an inhibitory mechanism generating curved saccade trajectories contributes to performing the task. In this paper, we investigate whether systematic curved saccades occur during search for a target object among dozens of scattered distractor objects. Visual search requires a sequence of saccades unless the target can be distinguished from the distractors by a basic feature. For the efficiency of serial visual search, observers should direct their eyes to the unexamined locations rather than the previously examined locations, because the reexamination of already-checked distractors is inefficient. Indeed, a couple of studies examining eye movements during serial visual search showed that there were fewer saccades returning to previously fixated locations than would be expected by chance (Gilchrist & Harvey, 2000; Peterson, Kramer, Wang, Irwin, & McCarley, 2001; see also, Hooge, Over, van Wezel, & Frens, 2005). One possible mechanism for prevention of refixations is inhibition of return to the previously fixated distractors (Müller & von Mühlenen, 2000; Takeda & Yagi, 2000; see Klein, 2000, for a review). It is possible that inhibition of return generates curved saccade trajectories, because the neural mechanism for inhibition of return as well as curved saccade trajectories involve the SC (Dorris, Klein, Everling, & Munoz, 2002; Fecteau & Munoz, 2005; Sapir, Soroker, Berger, & Henik, 1999).

Based on the account that inhibition to the previously fixated distractors may occur during serial visual search, it would be reasonable to expect that the saccade trajectories during serial visual search may curve under the influence of inhibition. However, the serial visual search task is different in several ways from the tasks used in the previous studies of the curved saccade. First, the goal and onset timing of saccades are voluntarily planned during serial visual search, while they were controlled by the imperative stimuli in the previous studies. Second, it is possible that multiple locations are inhibited during serial visual search, while only one location was inhibited in the previous studies. At present, we have little data on spatial and temporal interactions between inhibition of multiple locations, and their effect on the trajectory of voluntarily planned saccades. To address this issue, we investigated the relationship between the previously fixated locations and the saccade trajectories in serial visual search, and examined the nature of the inhibition of the previously examined locations by using the saccade trajectories as an index of spatial inhibition.

2. Method

2.1. Participants

Four male adults (30–33 years old), KY, HS, MS, and YT, participated in the experiment. HS and YT are the authors of the present paper. KY and MS were naïve to the purpose of the experiment, but were experienced with Eyelink II and visual search tasks from other experiments. HS and YT wore eyeglasses to correct visual acuity, while KY and MS had normal visual acuity. None showed any oculomotor pathology.

2.2. Apparatus

The experiment was controlled by a PC/AT compatible machine. A 17-in. cathode-ray tube (CRT) monitor was used for stimulus presentation. The participant sat on a chair with the head stabilized by a headrest and a chin rest. The CRT was placed in front of the participant at a dis-

tance of 72 cm; screen size was 24.8 deg × 18.6 deg of visual angle. The background of the screen was a uniform gray color throughout an experimental block. An Eyelink II eye tracker (SR Research Ltd.) was used for recording eye movements. The sampling rate of the eye tracker was 250 Hz. The Psychophysics toolbox (Brainard, 1997; Pelli, 1997) and the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002) were used for stimulus presentation and controlling the eye tracker. The keyboard connected to the PC was located in front of the participant for manual responses.

2.3. Stimulus and procedure

The eye tracker was calibrated and the data validated at the beginning of each experimental block, using the Calibration/Validation procedures of Eyelink II. During these procedures, the participant was asked to track a small circle that appeared at nine locations on the screen. The nine locations were the center, the corners and the midpoint of each of the four sides of the screen. The tracker was adjusted until the measurement error was less than 0.5 deg for the average of the nine locations. After calibration and validation, a small circle was presented at the center of the screen. The participant fixated on the circle and pressed the space key with his left index finger. The output of the eye tracker when the key was pressed was used by Eyelink II for correcting for head movement during an experimental block (“Drift Correction”). Immediately after pressing the space key, a search stimulus array was presented on the screen (Fig. 1). The search stimuli consisted of 16 items placed at randomly chosen locations on the nodes of an 8 × 8 invisible grid. The distances between adjoining grid nodes were 2.2 deg. The items were a circle and 15 arcs in 50% of the trials (target present trials), and 16 arcs in the remaining trials (target absent trials). The diameters of the items were 0.9 deg of visual angle. One-eighth of the circle was cut out as a gap to form each arc, and the location of the gap was at 0, 90, 180 or 270 deg. The participants were asked to press the “0” key with their right index fingers if a circle was present, and to press the space key with their left index fingers if no circle was present, as quickly and accurately as possible. This type of visual search task requires a sequence of saccades. When the participant pressed either key, the trial was finished and the drift correction for the next trial started automatically. One experimental block consisted of 50 trials, and five blocks were successively presented in a single session. Each participant completed five sessions.

2.4. Data analysis

For detection of the beginning and the end of a saccade, the data parser built in Eyelink II was used. Velocity and acceleration thresholds for detecting saccades were set to 22 deg/sec and 3800 deg/sec^2, respectively. To evaluate the curvature of saccade trajectories, we first normalized the saccades’ lengths to 1.0. Then we measured the “area curvature” (Ludwig & Gilchrist, 2002), the area that was enclosed by the saccade trajectory and a line between the start and end points of the saccade (Fig. 2A). The trapezoidal rule was used for calculating area. We refer to saccades that curved to the left viewing from the starting point of the saccade as “clockwise” (CW), and saccades that curved to the right as “counter-clockwise” (CCW).

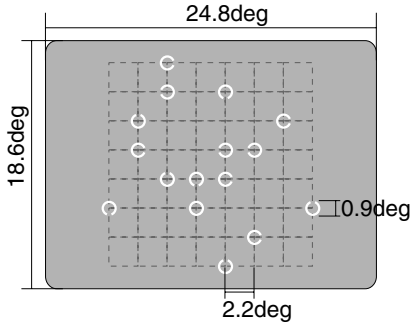

Fig. 1. Search stimulus used in the present experiment. Note that the grid lines were invisible in the actual display.

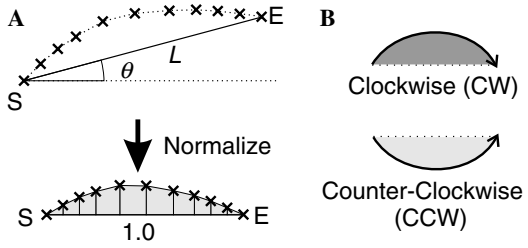

Fig. 2. (A) Definition of deviation of saccade trajectories by means of area curvatures. S, E, L and θ indicate the start and end of a saccade, saccade length, and saccade direction, respectively. (B) Classification of the deviation of saccade trajectories.

3. Results

3.1. Eye movements and search performance

In the total of the trials for each participant, 8508, 16065, 13679 and 13241 saccades were detected by the Eyelink II parser for KY, HS, MS and YT, respectively. The top row of Fig. 3 shows distributions of duration and curvature of the detected saccades (data of all subjects were pooled together). Approximately 8% of saccades (269, 1947, 1093 and 930 saccades for KY, HS, MS and YT, respectively) were shorter than 12 ms. These saccades were discarded because the sampling rate of 250 Hz was not

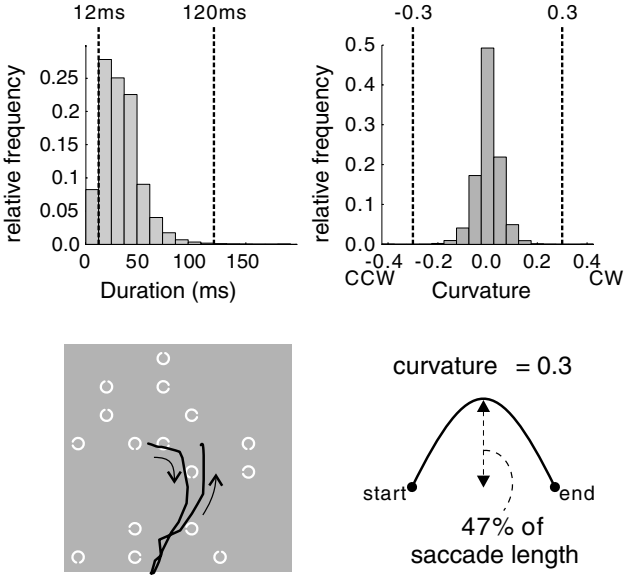

Fig. 3. (Top row) Distributions of duration and area curvature of detected saccades. Vertical dotted lines indicate the criterion for data rejection (data of all participants were pooled together). (Bottom left) An example of a saccade removed from data analysis. (Bottom right) If a trajectory is parabolic, area curvature of 0.3 means that the peak of the trajectory deviates approximately 47% of the saccade length from the line connecting the start and end points of the saccade.

sufficient to measure the area curvature of such short saccades. In addition, we found a small amount of data which the data parser of Eyelink II judged as a saccade but had atypical trajectories. An example of such data detected as a saccade is shown in Fig. 3 (bottom left panel). Such atypical data may be "re-directed" saccades (Godijn & Theeuwes, 2002; McPeek & Keller, 2001). That is, a sequence of multiple saccades with short inter-saccade intervals not detectable by the Eyelink II parser. To remove such atypical data, we visually inspected each data that had an unusual long duration or large area curvature, and found that the data with duration of more than 120 ms or an absolute area curvature of more than 0.3 were atypical. Approximately 0.6% of saccades (56, 146, 71 and 11 saccades for KY, HS, MS and YT, respectively) were discarded using these criteria. In total, 325 (3.8%), 2093 (13.0%), 1164 (8.5%) and 941 (7.1%) saccades were removed because the duration or area curvature of the saccade exceeded our criterion.

Table 1 summarizes the error rate for manual responses, mean reaction time (RT), number of saccades in a single trial, and correlation between RT and number of saccades for each participant. For all participants, the mean RT was obviously longer in the target absent trials than that in the target present trials, and the mean number of saccades in the target absent trials was approximately twice as many as in the target present trials. Furthermore, a high correlation between RT and number of saccades was observed (r was more than 0.87 in the target present trials and more than 0.61 in the target absent trials). These results are consistent with the account that participants serially deployed their attention to each item (or each cluster of items) during the visual search task.

Because we are interested in whether previously fixated locations influenced the ongoing saccade trajectory, it is desirable that a single trial contains as many saccades as possible. However, in the target-present trials, the participants often found the target circle so quickly that only a few saccades were executed before the key press ended the trial. It is difficult to deal with such shortly-terminated trials in the following analyses. Therefore, we used only the data from the target-absent trials in the following analyses. Furthermore, 13.5%, 29.9%, 24.0% and 23.7% of the detected saccades were shorter than 2.2 deg for KY, HS, MS and YT, respectively, which was the minimum horizontal or vertical distance between items. Most of these saccades were probably corrective saccades (Becker & Fuchs, 1969; Findlay, Brown, & Gilchrist, 2001), and it would be better not to handle these saccades in the same way as the longer saccades. In the following analyses, we merged the saccades shorter than 2.2 deg with the fixations. Because of these data manipulations, we had samples of 4614, 6141, 6354 and 6163 saccades for KY, HS, MS and YT, respectively.

Table 1
Error rate for manual responses, mean reaction time, mean number of saccades in a single trial and correlation between reaction time and number of saccades

Subject	Error rate (%)	Reaction time (s)	Number of saccades	Correlation (r)
Target present				
KY	5.73	1.03 (0.39)	3.52 (1.77)	0.89
HS	4.13	1.74 (0.72)	5.98 (3.35)	0.89
MS	4.53	1.23 (0.53)	5.08 (2.67)	0.87
YT	1.33	1.61 (0.73)	5.33 (2.87)	0.93
Target absent				
KY	1.73	1.75 (0.38)	7.18 (1.84)	0.83
HS	0.93	3.26 (0.64)	12.46 (2.88)	0.61
MS	2.67	2.51 (0.69)	11.56 (3.13)	0.89
YT	0.00	3.04 (0.45)	11.0 (1.84)	0.627

Note: Numbers in parenthesis indicate the standard deviations.

To confirm that the participants serially fixated on the different parts of the stimulus array in a single trial, we plotted the relative frequency of distances between the goal of the next saccade and the 12 previous fixations (Fig. 4). The horizontal white dashed lines in Fig. 4 indicate the distance of 2.2 deg, which is the minimum distance between the centers of items. The distances between the goal of the next saccade and the previous fixation gradually increased for the first 4–6 saccades. Importantly, the distance was rarely less than 2.2 deg for the eight previous fixations. The frequencies of saccades directed to a location near the previous fixations (<2.2 deg) were 2.9%, 3.5%, 5.4%, and 2.3% for KY, HS, MS, and YT, respectively. These results are consistent with the account that directing the gaze toward the previously fixated locations was inhibited, although it remains possible that observers scanned visual items strategically without any inhibitory process.

3.2. Relationship between saccade trajectory and previously fixated locations

To examine whether there is any relationship between the saccade trajectory (CW vs. CCW saccade) and the previously fixated locations, we normalized saccade length and direction, and transformed the previously fixated locations with respect to the normalized saccade. Fig. 5 illustrates the procedure of normalization for the following analysis. Fig. 5A shows an example of recorded saccade trajectories. A red trajectory is a saccade to the present focus. Yellow trajectories are previous saccades, and blue points are previously fixated locations. To express the likely locations of previous fixations, we constructed a two-dimensional map by replacing the starting points of each previous saccade with a Gaussian function and summing them up (Fig. 5B). The mathematical definition of this "fixation map" is

$$\sum_i G(FX_i, FY_i, s, s), \tag{1}$$

where $G(m_x, m_y, s_x, s_y)$ is a two-dimensional Gaussian function whose mean is (m_x, m_y) and standard deviation is (s_x, s_y). (FX_i, FY_i) is the center of the ith previously

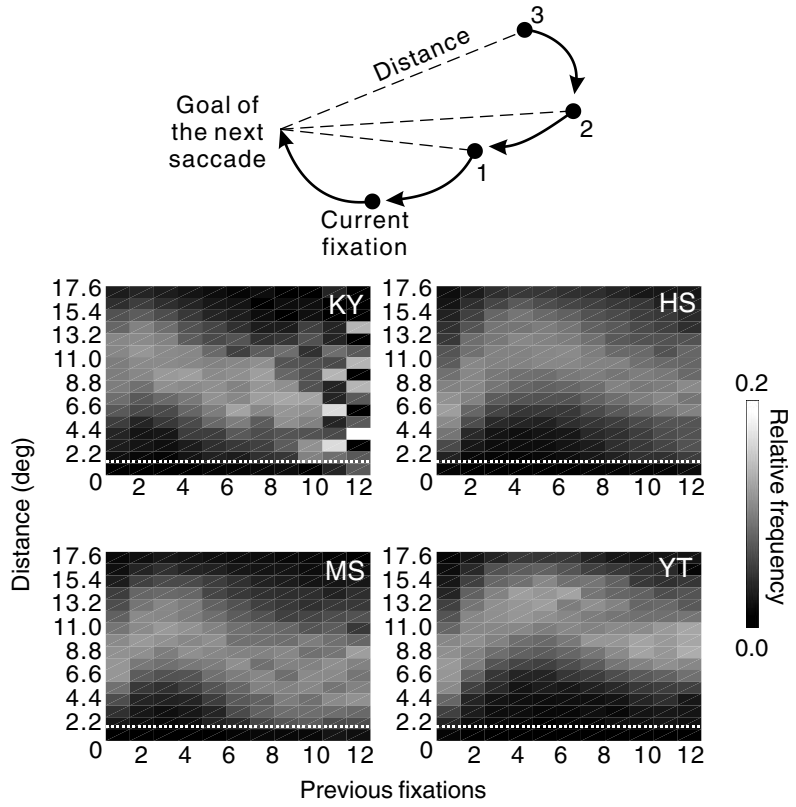

Fig. 4. (Top panel) Definition of the distance between the goal of the next saccade and the previous fixations. Three previous fixations are shown here. Filled circles at the end of the trajectories indicate the saccade start points. (Bottom panel) Relative frequency of the distance between the goal of the next saccade and the previous fixations, separately calculated for the first to twelfth previous fixations. Dashed white horizontal lines indicate the minimum distance between items (2.2 deg). Note that data of the 10–12 previous fixations for KY was noisy because KY made fewer saccades in a single trial compared to other subjects (see Table 1).

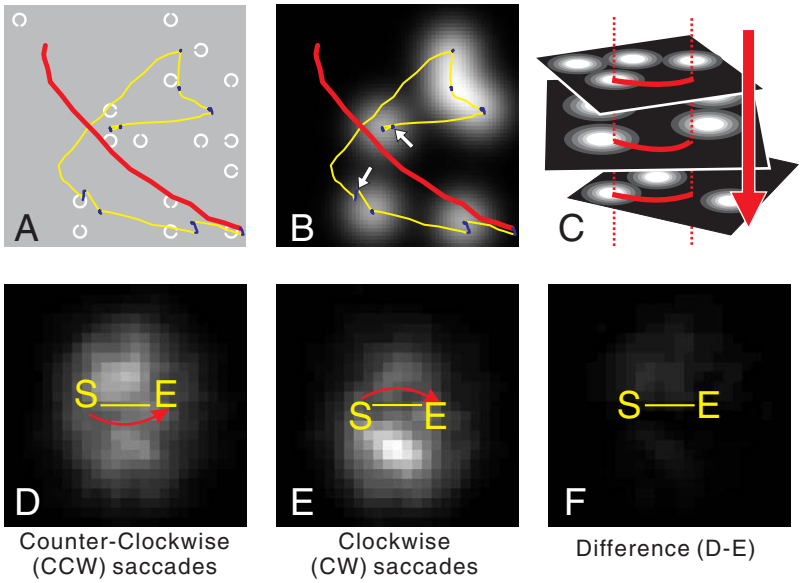

Fig. 5. The procedure for calculating the fixation map. (A) An example of a saccade trajectory. Red trajectory indicates the saccade under analysis. Yellow trajectories indicate previous saccades. Blue points indicate previously fixated locations. (B) The fixation map for a single saccade. White arrows indicate saccades that are merged with fixation because the saccade length is less than 2.2 deg. (C) Fixation maps are normalized so that length and direction of the saccades are the same and averaged over trials. (D) An example of an averaged fixation map for counter-clockwise saccades. A yellow line segment indicates the normalized start and end points of the saccade. Yellow S and E indicate the start and end points of the saccade, respectively. (E) An example of an averaged fixation map for clockwise saccades. (F) Differences between fixation maps for counter-clockwise and clockwise saccades. Red and blue areas indicate positive and negative values, respectively. Red areas indicate likely locations of the previous fixations for counter-clockwise saccades, and blue areas indicate those for clockwise saccades.

fixated location, and s is fixed to 2.2 deg. As previously described, saccades shorter than 2.2 deg (i.e., minimum horizontal or vertical distance between items) were merged with fixation (white arrows in Fig. 5B), so that a location where there were many small corrective saccades would not be unreasonably influential. The obtained images were normalized by rotating and scaling the images so that the start and end points of saccades were transformed into $(0,0)$ and $(0,1)$, respectively. The normalized fixation map is

$$\sum_i G\left(Fx_i, Fy_i, \frac{s}{l}, \frac{s}{l}\right), \tag{2}$$

where (Fx_i, Fy_i) is the normalized center of the ith previously fixated location, and l is the length of the saccade. Then the data for the clockwise and the counter-clockwise saccades were averaged separately (Fig. 5C). Fig. 5D is an example of the average for all saccade data with a length of 4.4–13.2 deg and a counter-clockwise trajectory. The denser cloud in the upper half of the figure compared with the lower half of the figure suggests that the previously fixated locations were likely on the left side of the line connecting the start and end points of the saccade when the saccades had a counter-clockwise curvature. Fig. 5E shows an example of the average for all saccade data of 4.4–13.2 deg length and clockwise trajectory. Similar to Fig. 5D, a denser cloud is evident in the direction opposite to the curved saccade trajectory. Subtracting Fig. 5E from Fig. 5D, we obtain Fig. 5F. Red and blue areas indicate the likely previously fixated locations when the saccades had counter-clockwise or clockwise trajectories, respectively.

Before accepting the results of the fixation map analysis shown in Fig. 5, we have to consider the possibility that the relationship between saccade trajectories and previously fixated locations depends on saccade length, and that the normalization of saccade length distorted this relationship. To examine this possibility, we split the data into four groups with regard to saccade length. The ranges were 4.4–6.6, 6.6–8.8, 8.8–11.0 and 11.0–13.2 deg, corresponding to the distances of 2–3, 3–4, 4–5 and 5–6 grid nodes on the search display. The top row of Fig. 6 shows the means and standard deviations of the area of the curvature within these ranges of saccade length. The four columns

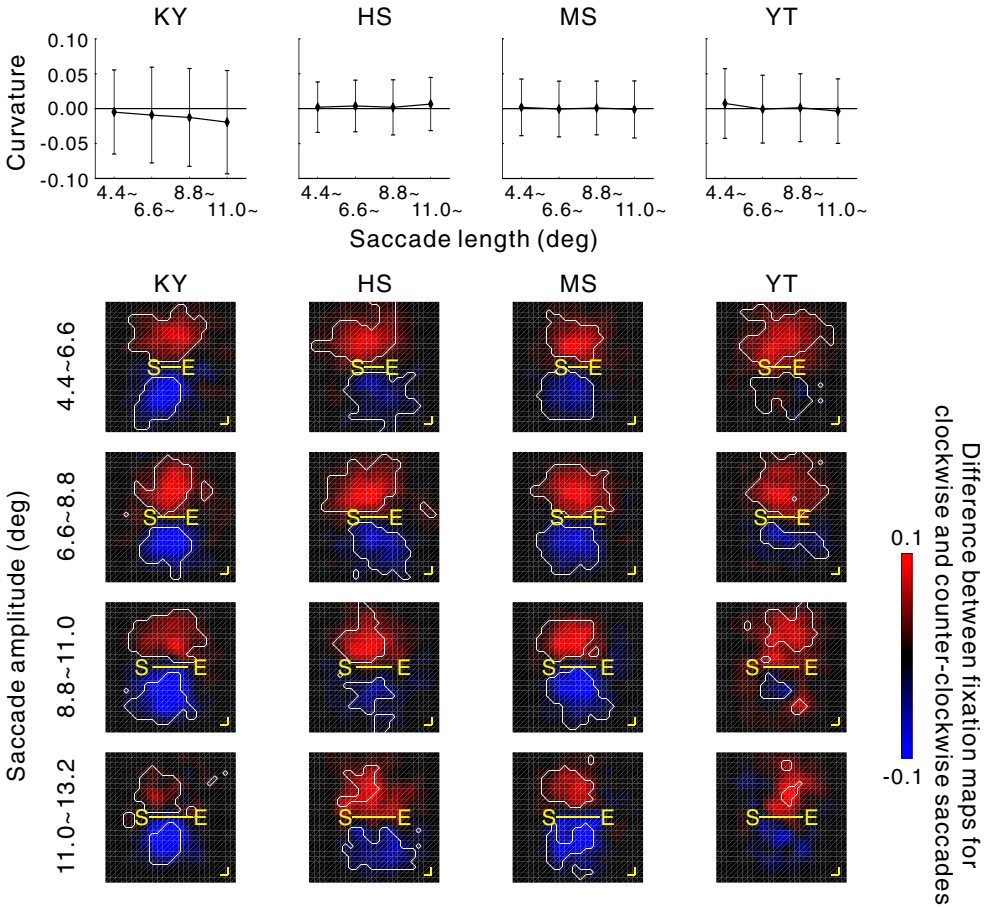

Fig. 6. (Top row) The mean area curvatures plotted against saccade length. Error bars represent the standard deviations. (Second to fifth rows) The difference of fixation maps between counter-clockwise and clockwise saccades. Maps were averaged separately for the four subjects and the four ranges of saccade lengths. Yellow "S" and "E" indicate the start and end points of the saccades, respectively. The yellow angle at the right-bottom of each plot is a scale that represents the minimum distance between items (2.2 deg). The area enclosed by thin white lines indicates that the value of the map was significantly different from zero (pixel-wise t test, $p < .01$). Red and blue areas in the upper and bottom part of each plot indicate that the previously fixated locations were likely to exist in the direction opposite to the curved saccade trajectories.

correspond to the four participants. Inspection of Fig. 6 suggests that the mean area curvature did not systematically depend on saccade length. Moreover, the standard deviation also did not show a systematic dependency on saccade length. The second to fifth rows of Fig. 6 show the difference (CCW − CW) of fixation maps for each range of saccade length. The areas enclosed by thin white lines indicate that the difference of the fixation maps is significantly different from zero (pixel-wise t test, $p < .01$). In all plots, red areas are dominant in the upper part of the plot, and blue areas are dominant in the lower part. This result suggests that saccade trajectories tended to curve away from the side of the previous fixation regardless of saccade length. To compare the shape of the red and blue areas, we fitted the following function to the difference of fixation maps (see also Appendix A):

$$f(x,y) = c\big(G(x-m_x, y-m_y, s_x, s_y) - G(x-m_x, y+m_y, s_x, s_y)\big) + d. \quad (3)$$

$G(x - m_x,\ y - m_y,\ s_x,\ s_y)$ is a two-dimensional Gaussian function whose mean is $(m_x,\ m_y)$ and standard deviation is $(s_x,\ s_y)$. c determines amplitude of the function. d is a bias term. We used the NonlinearRegress function of Mathematica 5.2 (Wolfram Research) to estimate m_x, m_y, s_x, s_y, c, and d separately for each range of saccade length. Fig. 7 shows the results of the regression analysis. The top row illustrates shapes of the best-fit function (data of all saccade lengths were pooled), and the second to fourth rows show estimated values of peak location, peak height, and half-peak width for each saccade length, respectively. The peak and half-peak were calculated after the bias term (d) was removed. Inspection of Fig. 7 suggests that none of the parameters depended systematically on saccade length. In conclusion, saccade trajectories curved in the direction where there were fewer previously fixated locations, for all ranges of saccade lengths we examined.

The fixation map analysis suggests that the sign of the area curvature (i.e., CW vs. CCW) is substantially related to previously fixated locations. However, there remain some factors to resolve. First, in addition to the attentional factor, the direction of the saccade also strongly influences its trajectory. Viviani, Berthoz, and Tracey (1977) reported that right-down and left-up saccades have clockwise curvature, while right-up and left-down saccades have counterclockwise curvature. The effect of saccade direction on its trajectory is considered to be caused by a physiological mechanism for saccade generation (Leigh & Zee, 1999). We inspected our data (see Fig. 8) and found that the area curvature depended on the saccade direction, similar to the observation of Viviani et al. (1977). It is necessary to remove this factor in order to reveal the relationship between saccade trajectory and previously fixated locations. Second, we used all the previous fixation locations

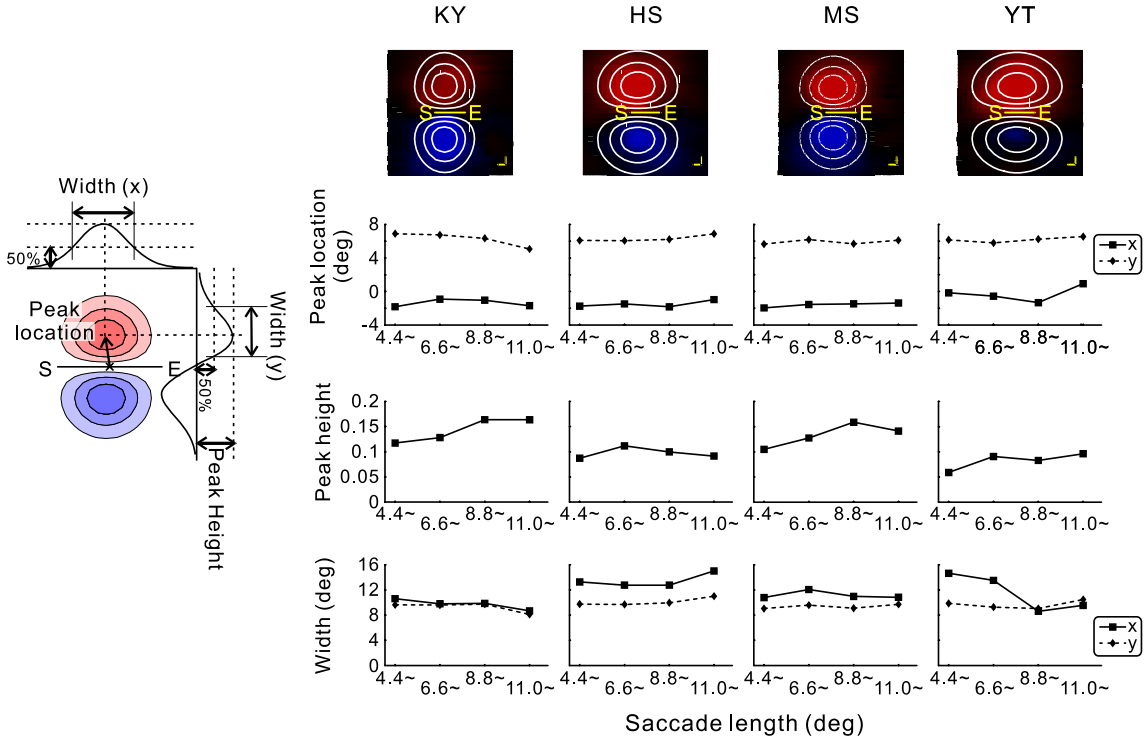

Fig. 7. Fitting Eq. (3) to the difference between the CW and CCW fixation maps. (Left panel) Definition of the peak location, peak height and width of the best-fit function. The peak location was measured from the midpoint between the start point (S) and the end point (E). (Top row) The best-fit function plotted on the data (data of all saccade length were pooled). White lines were the contour plot of the best-fit function (75%, 50% and 25% points of the positive and negative peak were plotted). See Fig. 6 for yellow characters and lines. Second to fourth rows: Peak location, peak height, and width of the best-fit function plotted against four ranges of saccade length. The four columns correspond to the four participants.

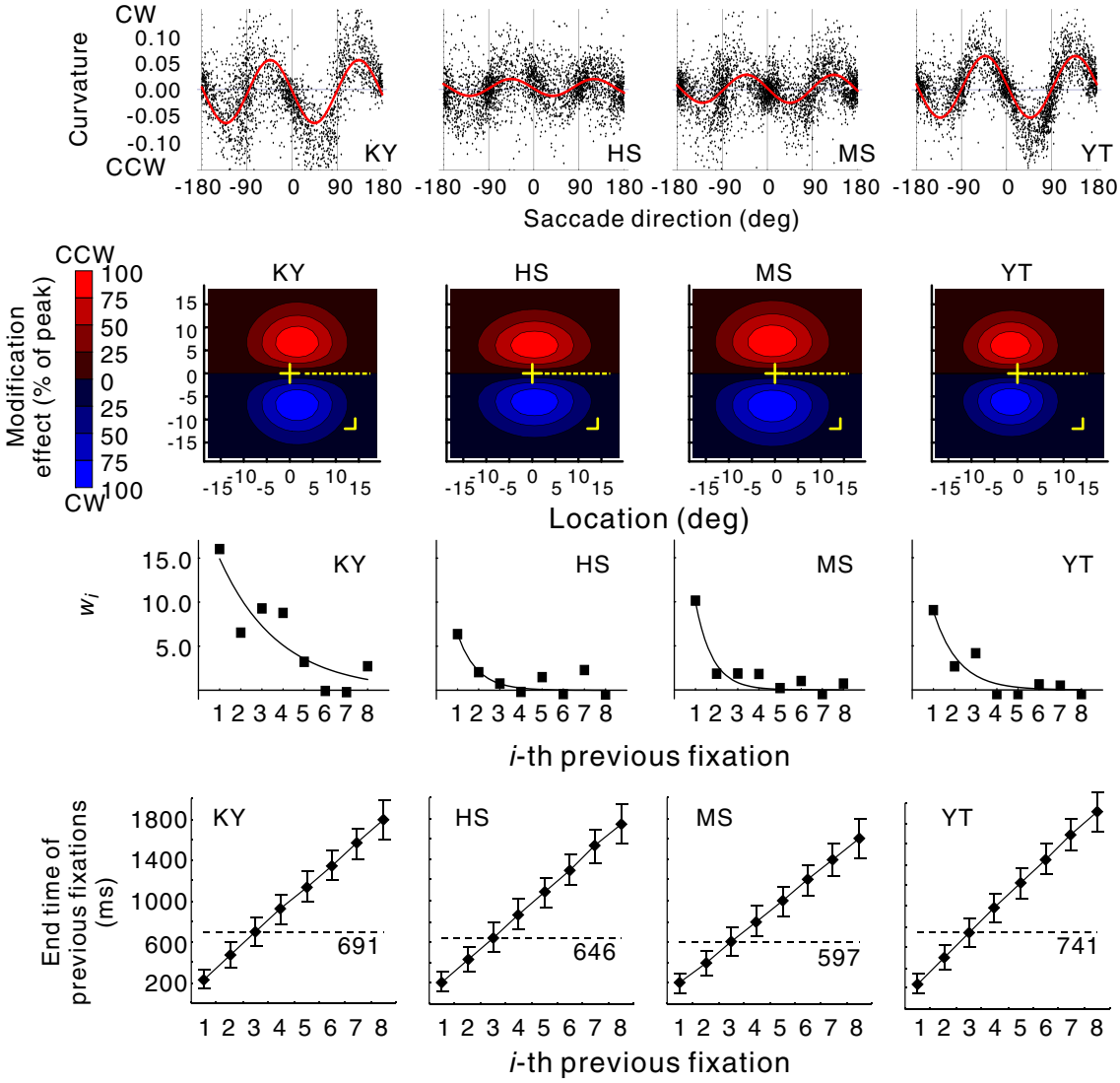

Fig. 8. (Top row) Curvature of saccade trajectories plotted against saccade direction. Red curves indicate the saccade-direction dependent component of the model (Eq. (7)). (Second row) Contour plot of the modification field estimated by the model. The yellow cross and dotted line represent the saccade start point and the saccade direction, respectively. The yellow angle at the corner of each plot represents a 2.2×2.2 deg scale. (Third row) The weight for the ith previous fixations (w_i), plotted against i. (Bottom row) The mean time difference between the saccade onset and the end of the ith previous fixation plotted against i. The error bars represent the standard deviations. Horizontal dashed lines with a number indicate the mean end time of the third previous fixation from the saccade onset time.

to draw the fixation maps. However, it is likely that the most proximal fixation affects the saccade trajectory more strongly than previous fixations. To examine the effect from previous fixated locations on saccade trajectory in detail, we performed a regression analysis.

3.3. Regression analysis

To perform a regression analysis, we had to build a model that represents how previous fixations influence saccade trajectories. In the following analysis, we examined how effectively a simple model explains variations of area curvature of saccades rather than trying to build a complete model for generating curved saccade trajectories.

We made three assumptions in our model. The first assumption was that the effect of saccade direction would be proportional to the sine of the saccade direction. This assumption can be modeled as follows:

$$q_1 \sin(q_2\theta + q_3), \tag{4}$$

where θ represents saccade direction in radian. q_1, q_2 and q_3 are parameters estimated by regression. The second assumption was that there was a "modification field" spreading along the line connecting the start and end points of the saccade, which makes the saccade curve away from previous fixations if the previous fixations are in the field. The shape of the modification field would be independent of saccade length, and approximated by a difference of two-dimensional Gaussian functions. In order to simplify

this model, we assumed that the shape of the modification field was constant across time, and the total modification effect was calculated by the weighted summation of modification effects of each previous fixation. From these assumptions, the effect of the ith previous fixation on the area curvature of the saccade was modeled as follows:

$$w_i f(FX_i, FY_i). \tag{5}$$

(FX_i, FY_i) is the ith previous fixation location, which is rotated so that the saccade direction is aligned at zero degree (i.e., rightward horizontal) but not scaled as we did when we drew the fixation map. w_i represents the strength of modification effect of the ith previous fixation. f is defined by following equation:

$$f(x,y) = G(x - m_x, y - m_y, s_x, s_y) - G(x - m_x, y + m_y, s_x, s_y), \tag{6}$$

where $G(x - m_x,\ y - m_y,\ s_x,\ s_y)$ is a two-dimensional Gaussian function whose mean is $(m_x,\ m_y)$ and standard deviation is $(s_x,\ s_y)$. The final assumption is that the effect of saccade direction (Eq. (4)) and the ith previous fixation (Eq. (5)) would be integrated by linear summation. Summing Eq. (4) with (5), we obtain

$$\kappa = C + q_1 \sin(q_2\theta + q_3) + \sum_{i=1}^{8} w_i f(FX_i, FY_i). \tag{7}$$

Here, we did not consider the effect of more than eight previous fixations. Therefore, the upper limit of the sum was set to eight. If the saccade had less than eight previous fixations, we set $(0,0)$ for the location of the lacking previous fixations. From the definition of $f(x,y)$ (Eq. (6)), substituting $(0,0)$ for $(FX_i,\ FY_i)$ makes the contribution of the lacking previous fixation zero. C is a bias in the saccade curvature. $FX_{1\text{–}8}, FY_{1\text{–}8}$ and θ were the input variables, and C, q_1–q_3, w_1–w_8, m_x, m_y, s_x, and s_y were the parameters to be estimated.

We used the NonlinearRegress function of Mathematica 5.2 (Wolfram Research) with the Levenberg–Marquardt algorithm for nonlinear regression. Because the nonlinear fitting algorithm often diverged or fell in local minima, we calculated fitting parameters for 100 sets of initial values randomly generated from an interval of −10.0 to 10.0, and selected the parameters that gave the best fitting performance (however, the initial value of q_2 and q_3 was fixed at 2.0 and 0.0 because randomizing these values frequently resulted in a failure of analysis). We used saccades of 4.4–13.2 deg length for the analysis. The first saccade in each trial was removed from the data analysis because it has no previous fixation.

We evaluated performance of the regression analysis by the ratio of the difference between the corrected total sum of squares and the residual sum of squares to the corrected total sum of squares (this is comparable to R^2 produced by linear regression analysis). This ratio was 0.50, 0.24, 0.25, and 0.57 for KY, HS, MS, and YT, respectively. These values mean that 24–57% of the variance was explained by the model. These performances were better than the model without the factor of previous fixations, see Appendix B for detail. Fig. 8 shows the parameters estimated by the model. The top row plots area curvature against saccade direction. Red curves show the effect of saccade direction estimated by the model (Eq. (4)). The estimated values of q_2 and q_3 were approximately 2.0 (2.00–2.17) and 0.0 (−0.08 to 0.13), respectively, indicating that the estimated curves had a wavelength of π and no phase shift. Furthermore, the estimated value of C was approximately 0.0 (−0.004 to 0.005), indicating that there was little bias of curved saccade trajectories for a specific direction (i.e., CW and CCW saccades occurred with equal probability). The second row plots the profile of the estimated modification field. Previous fixation points in the blue area made saccades curve clockwise, and those in the red area made saccades curve counter-clockwise. The yellow cross indicates the start point of a saccade, and the yellow angle at the right-bottom of each plot is a scale that represents the minimum distance between items (2.2 deg). Considering our stimulus size (about 18 deg in height and width), the estimated modification field was enough large to cover almost all parts of the search stimulus when the start point of the saccade was near the center of the search display. The third row of Fig. 8 shows the estimated w_i, which represents how strongly the ith previous fixation modifies the area curvature of saccade trajectory. w_i was largest when $i = 1$ and steeply decreased to zero as i became larger. Although some variability was observed between participants, w_1–w_3 was positive for all participants, while two of the four participants showed negative values of w_4. This result suggests that at least the first to third previous fixation modified the saccade trajectory curve away from the fixated locations.

In the present model, we calculated the total modification effect using the weighted summation of modification effects of each previous fixation, namely we assumed that the strength of the modification effect varied depending on the number of intervening saccades rather than elapsed time. However, it is quite possible that the modification effect decreases with time. To evaluate the time course of the modification effect, we plotted time differences between the start of the saccade under analysis and the end of the previous fixations (the bottom row of Fig. 8). The time difference linearly increased, and the slope of the function was about 200–240 ms. The end of the third previous fixation was 691, 646, 597 and 741 ms before the start of the saccade for KY, HS, MS and YT, respectively. Therefore, we can say that the effect from previous fixation to saccade trajectory lasted for 600–750 ms.

In summary, both the effect of saccade direction and previous fixations on the curvature of saccade trajectory were confirmed by the regression analysis. The strength of the modification effect decreased with an increasing number of intervening fixations (or time), and at least the three previous fixations made the saccade trajectory curve away from those fixation locations.

4. Discussion

In most previous studies, the attentional modification of saccade trajectories has been investigated by using a spatial cueing paradigm in which participants were required to make a single saccade to the location indicated by a cue (e.g., Sheliga et al., 1995), or by using an efficient visual search paradigm in which participants were required to make a single saccade to a pop-out target (e.g., Godijn & Theeuwes, 2002). Therefore, we have little knowledge about the nature of curved saccade trajectories in the case where participants have to make saccades to multiple locations sequentially. In the present study, we investigated the saccade trajectories in an inefficient visual search task, which required serial gaze shifts. There are two important differences between the inefficient visual search task and the paradigms used in the previous studies. First, the goal and onset timing of saccades are voluntarily planned in the visual search task, while these were controlled by imperative stimuli in the previous studies. Second, it is possible that multiple locations were inhibited during serial visual search, while only one location was inhibited in the previous studies. Nevertheless, the present study found that the saccade trajectories during serial visual search are modified by the previously fixated locations, similar to previous findings using the imperative single saccade paradigm. Furthermore, the present study clarified that the saccade trajectories were affected by multiple locations (at least three recently fixated locations) in the manner of weighted summation. In the following sections, the nature of the curved saccade trajectories during serial visual search is discussed.

4.1. Spatial aspect of attentional modification

In the regression analysis, m_x, m_y, s_x, s_y, and w_1–w_8 were estimated as the parameters of the effect from previous fixations. The estimated parameters of m_x, m_y, s_x, and s_y indicate the spatial aspect of attentional modification, whereas those of w_1–w_8 indicate the temporal aspect of attentional modification. In this section, we discuss the spatial properties of attentional modification.

The spatial properties of attentional modification estimated in the model are summarized in the modification field (the second row of Fig. 8). The modification field is widely spread out parallel to the saccade path. The radius of the estimated modification field was more than 10 deg in all participants. These properties are compatible with previous studies of curved saccade trajectories using a single saccade paradigm. For example, Sheliga et al. (1995) presented four boxes in the diagonal directions at a distance of 6 deg from the fixation point, where a cue indicating an upward or downward saccade was presented. The results showed that the curved saccade occurred when the cue was presented either in the same or in the opposite (upper or lower) hemifield as the saccade goal. Tipper, Howard, and Paul (2001) replicated the results of Sheliga et al. (1995) by presenting the cue stimulus at a distance of approximately 12 deg from the fixation point. McSorley, Haggard, and Walker (2005) examined the effect of location of an onset distractor on saccade curvature. They found that an onset distractor presented more than 15 deg away from the saccade goal could modify the saccade trajectory, although individual differences between participants were observed. We consider that Eq. (7) is a simple model but able to outline the modification effect of previous fixations on saccade trajectories.

The range of the modification field was consistent with previous studies, but the center of the field may be inconsistent with those studies. The saccade curvature increased monotonically as the distance between an onset distractor and the saccade goal became closer for two of the four participants in the study of McSorley et al. (2005). Sheliga et al. (1995) and Tipper et al. (2001) showed that the saccade curved more widely when the cue was presented in the same hemifield as the saccade direction. The modification field can simulate this property by shifting the center of the Gaussian functions from the fixation point to the saccade goal in the direction of the saccade. However, the center of the modification field estimated from the present data showed no systematic shift. Namely, two participants (KY and HS) showed a small shift of the modification field in the saccade direction, but the other two participants (MS and YT) showed a small shift in the opposite direction. One possible explanation for the inconsistency between the results in the previous studies and the estimated modification field in the present study is as follows. In the serial visual search task, participants tended to perform saccades directed to the location far from previous fixations (see Fig. 4). Therefore, it is plausible that there were more previous fixated locations opposite to the direction of the saccade goal than in the same direction. These previously fixated locations may influence the center of the modification field. It is also possible that there are nonlinear interactions between inhibitions for previous fixations that are not considered by the present model. Further research is necessary to clarify this issue.

4.2. Temporal aspect of attentional modification—saccade curves vs. inhibition of return

In this section, we discuss the temporal properties of attentional modification. Temporal properties of the effect from a previous fixation on saccade trajectory could be estimated as w_1–w_8 in the present model (Eq. (7)). As shown in the third row of Fig. 8, the effects (w_i) decreased with increasing intervening fixations or time. Although some variability was observed between participants, the saccade trajectories were influenced by at least three previous fixations, which corresponds to an interval of 600–750 ms (see bottom row of Fig. 8). There is no direct evidence whether the decrease of effect was caused by the intervening fixations or by time. However, a time-dependent function is plausible, because the time course estimated in the present study was similar to that observed in a

previous study using a single saccade paradigm (Godijn & Theeuwes, 2004). In Godijn and Theeuwes, an abrupt onset distractor, which should be ignored, was presented, and then a saccade cue that indicated the direction of the saccade was given. The stimulus onset asynchrony (SOA) between the distractor and the saccade cue was manipulated in the range of 100–800 ms. They found that the saccade trajectory curving away from the distractor significantly decreased with increasing SOA, and only a small effect remained in the SOA 800 ms condition. This time course is consistent with the results in the present study, namely the inhibitory effect significantly decreased but lasted for 600–750 ms. In Godijn and Theeuwes, it is clear that the effect decreased with time, because no other distractor was given during the interval. Therefore, we consider it likely that the inhibitory effect of generating curved saccade trajectories during visual search decreases with time but not with intervening fixations.

Before examining the temporal properties of attentional modification, we had considered that the inhibitory mechanism generating curved saccade trajectories was closely related to "inhibition of return" (IOR). Many previous studies have proposed that IOR plays an important role for preventing reexamination during serial visual search (Klein & MacInnes, 1999; Kristjánsson, 2000; Müller & von Mühlenen, 2000; Peterson et al., 2001; Shore & Klein, 2000; Takeda, 2004; Takeda & Yagi, 2000; von Mühlenen, Müller, & Müller, 2003; see also Horowitz & Wolfe, 1998, 2001, 2003). However, similar to the findings in Godijn and Theeuwes (2004), the results in the present study also indicate that the temporal function of curved saccade trajectories is different from that of IOR. The temporal function of IOR has been examined by using a spatial cueing paradigm. In the typical spatial cueing paradigm, an abrupt onset cue, which is irrelevant to the target location, is presented, and then a target is given. Participants are required to make GO/NO-GO responses to the target appearance (a simple detection task). In this case, a facilitative effect for the cued location was observed when the SOA between the cue and the target was shorter than 300 ms, and the inhibitory effect (i.e., IOR) was observed when the SOA was longer than 300 ms (e.g., Posner & Cohen, 1984). Regarding the duration of IOR, it has been reported that an inhibitory effect could be observed in a SOA 1500 ms condition (Tassinari, Biscaldi, Marzi, & Berlucchi, 1989). Furthermore, it has been demonstrated that an inhibitory effect does not occur until a SOA of 700 ms when a target discrimination task (e.g., participants were required to respond whether the target was red or yellow) was used to examine the time course of IOR (Lupiáñez, Milan, Tornay, Madrid, & Tudela, 1997). Because the serial visual search performed in the present study involved discrimination processes, namely participants had to determine whether the attended item was a target or a distractor, it is plausible that IOR occurred 700 ms after leaving fixated locations. In this view, a possible mechanism of inhibition during serial visual search is that the inhibition generating curved saccade trajectories would arise immediately after the gaze shift and last for 600–750 ms. Then the inhibition generating IOR would arise concurrently with the decay of the previous inhibitory effect.

The temporal properties of curved saccade trajectories and IOR suggest a new hypothesis about the inhibitory mechanism during serial visual search. Namely, both inhibition generating curved saccade trajectories and IOR function with different time courses to prevent refixation during serial visual search. One of the arguments against the account that IOR prevents refixation during serial visual search concerns the temporal property of IOR (Horowitz & Wolfe, 2001; see also Dodd, Castel, & Pratt, 2003). As described above, IOR in the discrimination task arises 700 ms after the onset of the cue. If the temporal function of IOR during serial visual search was the same as that obtained in a discrimination task, three or four recently fixated locations would not be inhibited to prevent refixations. To explain this phenomenon, we speculate that two different inhibitory processes accomplish the control of gaze shifts during serial visual search. One is the inhibition generating curved saccade trajectory, and the other is the inhibition generating IOR. The results in the present study showed that at least three recently fixated locations affected the saccade trajectories in an inhibitory manner (see third row of Fig. 8). Although there is no evidence that this inhibition affects the selection of the saccade goal as well as the saccade trajectories during serial visual search, it is possible that preventing refixation is accomplished by this inhibitory mechanism before IOR arises. Further studies are needed to examine this speculation.

4.3. Limit of the model

As described in the previous sections, our model provides consistent results for the spatial and temporal influence of attentional modification on saccade trajectory. However, the performance of the model in the regression analysis was not highly predictive. As mentioned in the Results section, the performance of the model was 0.50, 0.24, 0.25, and 0.57 in terms of R^2 for KY, HS, MS, and YT, respectively. This indicates that the model could not explain 43–76% of the variance of the area curvature. Although it is not our purpose in the present paper to propose a complete model predicting the curved saccade trajectory, we discuss the possible factors reducing the performance in the regression analysis in this section.

We consider that the residual variance in the regression analysis resulted from at least three factors. The first factor is artifacts in measuring eye movements. In general, measuring eye movements often involves artifacts such as change of pupil area due to eyelid movement. Because the area curvature of the saccade trajectory was a very small signal relative to the saccade length, the larger artifacts in measuring eye movements could contribute to part of the residual variance.

The second factor is the shift of the saccade endpoint. As pointed out by Godijn and Theeuwes (2004), spatial inhibition makes not only the saccade trajectory, but also the endpoint of the saccade, shift away from the inhibited location. If this shift of the saccade endpoint occurred in the present experiment, then the area curvature would reflect only a part of the modification effect of the inhibition on the saccade trajectory. In the previous studies using a single saccade paradigm, the shift of the saccade endpoint is easily defined by the distance between the saccade endpoint and the instructed goal. However, it is difficult to define the shift of the saccade endpoint during serial visual search tasks, because there is no instructed saccade goal in a voluntary planned saccade. It is plausible that an underestimation of the inhibitory effect caused by a shift of the saccade endpoint reduced the performance of the regression analysis.

The final factor is the assumptions of the model. In the model, we only considered the effects from the saccade direction and the previous fixations on the trajectory of the curved saccade. However, previous studies suggest that variation of the area curvature of saccades cannot be fully explained by these factors. For example, Erkelens and Sloot (1995) studied variability of the initial direction and endpoint of oblique saccades. They asked the participants to make voluntary saccades between two targets on an imaginary circle of 20 deg radius. Variation in the trajectories of observed saccades was so large that the collection of saccade trajectories in a specific direction contained both clockwise and counter-clockwise saccades, although the median of the collection seemed to curve in a way similar to the results of (Viviani et al. (1977) and our present study (top row of Fig. 8). Moreover, several studies reported that trajectories of visually guided oblique saccades could curve in a way different from the results of Viviani et al. (Becker & Jürgens, 1990; see Quaia & Optican, 1997 for a brief review). Because the participants were not required to inhibit shifting spatial attention to a location other than the saccade target, inhibitory control of spatial attention probably had nothing to do with the variability of saccade trajectory in these studies. We speculate that factors other than the sine of the direction of the saccade influence the deviation of saccade trajectory. It would be necessary to build these unknown factors into the model to improve the performance of the model; however, this issue is beyond the scope of the present study.

4.4. Summary

In the present study, we examined whether saccades curve away from previous fixations during a serial visual search task. The results suggest that an inhibitory mechanism underlying the curved saccades functions during the serial visual search task. The effect from the previous fixations on saccade trajectories decreased exponentially related to the number of previous fixations. This modification effect was almost extinguished when the previous fixations ended 600–750 ms before the saccade onset, while approximately 700 ms was necessary for IOR in the discrimination task. The inhibitory mechanism underlying the curved saccades possibly works in conjunction with IOR in inhibiting saccades from returning to previously fixated locations.

Appendix A. Nonlinear estimation of width of the distribution of previous fixations

We used the difference of two Gaussian functions (DoG: Eq. (3)) to estimate the shape of the difference map between CW and CCW saccades. However, there is no theoretical reason to consider that the DoG is appropriate to fit the difference map. Therefore, we estimated the width of the difference map with a nonparametric method. Firstly, we calculated absolute difference maps between CW and CCW maps and averaged their columns and rows. Next, we estimated x-width by the number of columns that were above half of the highest column. y-width was estimated in a similar way but upper half of the rows were flipped and summed with the lower half of the rows before identifying the highest row. The bottom panel of Supplementary Fig. A1 plots the parametric width estimation using Eq. (3) against the nonparametric width estimation. The parametric estimation corresponds well with the nonparametric estimation. The correlation was 0.78 for x-width and 0.47 for y-width. Removing an outlier indicated by an arrow, the correlation reached 0.79 for y-width. (The outlier is 8.8–11.0 deg of Subject YT. As shown in Fig. 6, the red area as well as the blue area appeared in the lower part.) This result supports our decision to use the DoG function to fit the difference maps.

Appendix B. Performance of the model without considering the previous fixations factor

Because our model (Eq. (7)) includes both saccade direction and previous fixations factors, it is unclear what proportion of the variance is explained by saccade direction alone. To address this issue, we examined a model that does not use previous fixations. This model is given by following equation:

$$\kappa = C + q_1 \sin(q_2\theta + q_3). \tag{B.1}$$

For simplicity, we refer to Eqs. (B.1) and (7) as "Dir" and "Dir + Fix" models, respectively. Performances of these models cannot be directly compared because the Dir model has only four parameters while the Dir + Fix model has 16 parameters. To overcome this difficulty, we compared goodness of fitting with "likelihood ratio" (Dixon, 2003; Glover & Dixon, 2004). The likelihood ratio (λ) between the Dir and Dir + Fix model is defined as

$$\lambda = \mathrm{Exp}(k_{\mathrm{Dir}} - k_{\mathrm{DirFix}}) \left(\frac{\mathrm{SSE}_{\mathrm{Dir}}}{\mathrm{SSE}_{\mathrm{DirFix}}} \right)^{n/2}, \tag{B.2}$$

where k_{Dir} and k_{DirFix} are number of parameters in the Dir and Dir + Fix model; Exp is an exponential function;

SSE_{Dir} and SSS_{DirFix} are the sum of square error for the Dir and Dir + Fix model; and n is number of samples. $\lambda > 1$ means that the Dir + Fix model is better than the Dir model. We calculated λ for each subject and obtained 2.13×10^{151}, 8.68×10^{125}, 1.91×10^{114}, and 4.21×10^{111} for KY, HS, MS and YT, respectively. These values suggest that the Dir + Fix model is better than the Dir model. That is, the model including previous fixations provides a better *explanation* for the data.

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2006.07.003.

References

Aizawa, H., & Wurtz, R. H. (1998). Reversible inactivation of monkey superior colliculus. I. Curvature of saccade trajectory. *Journal of Neurophysiology, 79*, 2082–2096.

Becker, W., & Fuchs, A. F. (1969). Further properties of the human saccadic system: Eye movements and correction saccades with and without visual fixation points. *Vision Research, 9*, 1247–1258.

Becker, W., & Jürgens, R. (1990). Human oblique saccades: Quantitative analysis of the relation between horizontal and vertical components. *Vision Research, 30*, 893–920.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*, 433–436.

Cornelissen, F. W., Peters, E., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments and Computers, 34*, 613–617.

Dixon, P. (2003). The *p*-value fallacy and how to avoid it. *Canadian Journal of Experimental Psychology, 57*, 189–202.

Dodd, M. D., Castel, A. D., & Pratt, J. (2003). Inhibition of return with rapid serial shifts of attention: Implications for memory and visual search. *Perception & Psychophysics, 65*, 1126–1135.

Dorris, M. C., Klein, R. M., Everling, S., & Munoz, D. P. (2002). Contribution of the primate superior colliculus to inhibition of return. *Journal of Cognitive Neuroscience, 14*, 1256–1263.

Doyle, M., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research, 139*, 333–344.

Doyle, M., & Walker, R. (2002). Multisensory interactions in saccade target selection: Curved saccade trajectories. *Experimental Brain Research, 142*, 116–130.

Erkelens, C. J., & Sloot, O. B. (1995). Initial directions and landing positions of binocular saccades. *Vision Research, 35*, 3297–3303.

Fecteau, J. H., & Munoz, D. P. (2005). Correlates of capture of attention and inhibition of return across stages of visual processing. *Journal of Cognitive Neuroscience, 17*, 1714–1727.

Findlay, J. M., Brown, V., & Gilchrist, I. D. (2001). Saccade target selection in visual search: The effect of information from the previous fixation. *Vision Research, 41*, 87–95.

Gilchrist, I. D., & Harvey, M. (2000). Refixation frequency and memory mechanisms in visual search. *Current Biology, 10*, 1209–1212.

Glover, S., & Dixon, P. (2004). Likelihood Ratios: A simple and flexible statistics for empirical psychologists. *Psychonomic Bulletin & Review, 11*, 791–806.

Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance, 28*, 1039–1054.

Godijn, R., & Theeuwes, J. (2004). The relationship between inhibition of return and saccade trajectory deviations. *Journal of Experimental Psychology: Human Perception and Performance, 30*, 538–554.

Guitton, D. (1991). Control of saccadic eye and gaze movements by the superior colliculus and basal ganglia. In R. H. S. Carpenter (Ed.), *Vision and visual dysfunction, Volume 8, Eye movements*. Boca Raton, FL: The Macmillan Press.

Hooge, I. T., Over, E. A., van Wezel, R. J., & Frens, M. A. (2005). Inhibition of return is not a foraging facilitator in saccadic search and free viewing. *Vision Research, 45*, 1901–1908.

Horowitz, T. S., & Wolfe, J. M. (1998). Visual search has no memory. *Nature, 394*, 575–577.

Horowitz, T. S., & Wolfe, J. M. (2001). Search for multiple targets: Remember the targets, forget the search. *Perception & Psychophysics, 63*, 272–285.

Horowitz, T. S., & Wolfe, J. M. (2003). Memory for rejected distractors in visual search?. *Visual Cognition 10*, 257–298.

Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences, 4*, 138–147.

Klein, R. M., & MacInnes, W. J. (1999). Inhibition of return is a foraging facilitator in visual search. *Psychological Science, 10*, 346–352.

Kristjánsson, A. (2000). In search of remembrance: Evidence for memory in visual search. *Psychological Science, 11*, 328–332.

Lefèvre, P., Quaia, C., & Optican, L. M. (1998). Distributed model of control of saccades by superior colliculus and cerebellum. *Neural Networks, 11*, 1175–1190.

Leigh, R. J., & Zee, D. S. (1999). *The neurology of eye movement* (third ed.). New York: Oxford University Press.

Lupiáñez, J., Milan, E. G., Tornay, F. J., Madrid, E., & Tudela, P. (1997). Does IOR occur in discrimination task? Yes, it does, but later. *Perception & Psychophysics, 59*, 1241–1254.

Ludwig, C. J. H., & Gilchrist, I. D. (2002). Measuring saccade curvature: A curve-fitting approach. *Behavior Research Methods, Instruments, and Computers, 34*, 618–624.

McPeek, R. M., & Keller, E. L. (2001). Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey. *Vision Research, 41*, 785–800.

McPeek, R. M., Han, J. H., & Keller, E. L. (2003). Competition between saccade goals in the superior colliculus produces saccade curvature. *Journal of Neurophysiology, 89*, 2577–2590.

McSorley, E., Haggard, P., & Walker, R. (2004). Distractor modulation of saccade trajectories: Spatial separation and symmetry effects. *Experimental Brain Research, 155*, 320–333.

McSorley, E., Haggard, P., & Walker, R. (2005). Spatial and temporal aspects of oculomotor inhibition as revealed by saccade trajectories. *Vision Research, 45*, 2492–2499.

Meredith, M. A., & Ramoa, A. S. (1998). Intrinsic circuitry of the superior colliculus: Pharmacophysiological identification of horizontally oriented inhibitory interneurons. *Journal of Neurophysiology, 79*, 1597–1602.

Müller, H. J., & von Mühlenen, A. (2000). Probing distractor inhibition in visual search: Inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance, 26*, 1591–1605.

Munoz, D. P., & Istvan, P. J. (1998). Laretal inhibitory interactions in the intermediate layers of the monkey superior colliculus. *Journal of Neurophysiology, 79*, 1193–1209.

Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*, 437–442.

Peterson, M. S., Kramer, A. F., Wang, R. F., Irwin, D. E., & McCarley, J. S. (2001). Visual search has memory. *Psychological Science, 12*, 287–292.

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–556). Hillsdale, NJ: Erlbaum.

Quaia, C., Aizawa, H., Optican, L. M., & Wurtz, R. H. (1998). Reversible inactivation of monkey superior colliculus. II. Maps of saccadic deficits. *Journal of Neurophysiology, 79*, 2097–2110.

Quaia, C., & Optican, L. M. (1997). Model with distributed vectorial premotor bursters accounts for the component stretching of oblique saccades. *Journal of Neurophysiology, 78*, 1120–1134.

Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians – Evidence in favor of a premotor theory of attention. *Neuropsychologia, 25*, 31–40.

Robinson, D. A. (1975). Oculomotor control signals. In G. Lennerstrand & P. Bach-y-Riga (Eds.), *Basic mechanisms of ocular motility and their clinical implications* (pp. 337–374). New York: Pergamon Press.

Sapir, A., Soroker, N., Berger, A., & Henik, A. (1999). Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nature Neuroscience, 2*, 1053–1054.

Schlag-Rey, M., Schlag, J., & Dassonville, P. (1992). How the frontal eye field can impose a saccade goal on superior colliculus neurons. *Journal of Neurophysiology, 67*, 1003–1005.

Segraves, M. A., & Goldberg, M. E. (1987). Functional properties of corticotectal neurons in the monkey's frontal eye fields. *Journal of Neurophysiology, 58*, 1387–1419.

Selemon, L. D., & Goldman-Rakic, P. S. (1988). Common cortical and subcortical targets of the dorsolateral prefrontal and parietal cortices in the rhesus monkey: Evidence for a distributed neural network subserving spatially guided behavior. *Journal of Neuroscience, 8*, 4049–4068.

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research, 98*, 507–522.

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research, 105*, 261–275.

Sheliga, B. M., Craighero, L., Riggio, L., & Rizzolatti, G. (1997). Effects of spatial attention on directional manual and ocular responses. *Experimental Brain Research, 114*, 339–351.

Shore, D. I., & Klein, R. M. (2000). On the manifestations of memory in visual search. *Spatial Vision, 14*, 59–75.

Sparks, D. L., & Mays, L. E. (1983). Spatial localization of saccade targets. I. Compensation for stimulation-induced perturbations in eye position. *Journal of Neurophysiology, 49*, 45–63.

Takeda, Y. (2004). Search for multiple targets: Evidence for memory-based control of attention. *Psychonomic Bulletin & Review, 11*, 71–76.

Takeda, Y., & Yagi, A. (2000). Inhibitory tagging in visual search can be found if search stimuli remain visible. *Perception & Psychophysics, 62*, 927–934.

Tassinari, G., Biscaldi, M., Marzi, C. A., & Berlucchi, G. (1989). Ipsilateral inhibition and contralateral facilitation of simple reaction time to non-foveal visual targets from non-informative visual cues. *Acta Psychologica, 70*, 267–291.

Tipper, S. P., Howard, L. A., & Paul, M. A. (2001). Reaching affects saccade trajectories. *Experimental Brain Research, 136*, 241–249.

Trappenberg, T. P., Dorris, M. C., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience, 13*, 256–271.

Viviani, P., Berthoz, A., & Tracey, D. (1977). The curvature of oblique saccades. *Vision Research, 17*, 661–664.

von Mühlenen, A., Müller, H. J., & Müller, D. (2003). Sit-and-wait strategies in dynamic visual search. *Psychological Science, 14*, 309–314.